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Relative fitness of imazamox-resistant common sunflower and prairie sunflower

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Resistance to imidazolinone (IMI) herbicides has been incorporated recently into domesticated sunflower through conventional breeding methods. However, there are concerns regarding gene flow of the IMI-resistance trait to wild species and possible accompanying ecological consequences. Hybrids of domesticated sunflower with both common sunflower and prairie sunflower were created, with and without the imazamox-resistance trait. The relative fitness of imazamox-resistant (IMI-R) hybrids was compared with their imazamox-susceptible (IMI-S) counterparts. Greenhouse experiments were conducted to study the growth of IMI-R and IMI-S common and prairie sunflower hybrids under noncompetitive conditions. The photosynthesis rate of IMI-S prairie sunflower was slightly higher than that of IMI-R plants. However, relative growth rate, net assimilation rate, leaf area, and total dry weight were similar in IMI-R and IMI-S common and prairie sunflower, whereas plant height of IMI-S hybrid was greater than that of IMI-R common sunflower hybrids. A replacement series study was conducted under field conditions in 2001 and 2002 to evaluate the relative competitiveness of IMI-R and IMI-S common and prairie sunflower. IMI-R and IMI-S hybrids of both sunflower species were equally competitive. The results suggest that, in the absence of IMI herbicides, genes controlling IMI-R do not reduce or increase the competitive ability of either common or prairie sunflower. Therefore, if the IMI-resistant trait is incorporated in these species, the frequency of IMI-resistance genes is unlikely to decrease, even in the absence of IMI selection pressure.

Nomenclature: Imazamox; common sunflower, *Helianthus annuus* L.; prairie sunflower, *Helianthus petiolaris* Nutt.

Key words: Fitness, gene flow, imidazolinone herbicides.

Herbicide-resistant crops (HRCs) have the potential to improve weed management by providing alternative management options. In addition, HRCs provide cost-effective and flexible weed management practices, favor the use of environmentally sound herbicides, and promote the use of reduced and no-tillage agriculture (Duke 1996). Despite HRC benefits, concerns have been raised regarding the development and commercial release of HRCs including: a decrease in the number of herbicides available, an increase in herbicide use, a reduction of nonchemical weed management practices, weed population shifts, HRC volunteer plants in subsequent crops, and gene flow of herbicide resistance to wild species (Arriola and Ellstrand 1996; Langevin et al. 1990; Snow and Moran-Palma 1997).

The transfer of resistance traits from HRCs to wild species is a major concern because it can result in weed biotypes that are more noxious and difficult to control (Ellstrand 1988; Manasse 1992). For example, glufosinate-resistant canola (*Brassica napus* L.) has hybridized with field mustard (*Brassica rapa* L.), and imazamox-resistant (IMI-R) wheat (*Triticum aestivum* L.) has hybridized with jointed goatgrass (*Aegilops cylindrica* Host.) (Brown and Brown 1996; Seefeldt et al. 1998). In addition, volunteer canola plants grown in proximity of glufosinate-resistant, imidazolinone (IMI)-resistant, and glyphosate-resistant canola fields showed multiple resistance to glyphosate, glufosinate, and imazethapyr (Hall et al. 2000).

Sunflower resistance to imidazolinone herbicides was discovered in 1998, and resistance was caused by a less-sensitive acetolactate synthase (ALS) enzyme (Al-Khatib et al. 1998). Resistance to IMI-inhibiting herbicides can be caused by substitutions of five amino acids on the ALS enzyme (Tranel and Wright 2002). Bruniard and Miller (2001) suggested that IMI resistance is controlled by a major gene (Imir1) with a semidominant effect and a second gene (Imir2) with a modifying effect when the major gene is present. Full resistance is only achieved by homozygosity of both genes (Imir1 Imir1, Imir2 Imir2). Therefore, heterozygotes for both genes (Imir1 imir1, Imir2 imir2) are partially resistant. In contrast, Hall et al. (2000) reported that resistance to IMI-inhibiting herbicides is conferred by two semidominant genes and the presence of either gene was sufficient to confer resistance.

Resistance to IMI-inhibiting herbicides has been incorporated recently into domesticated sunflower through conventional breeding methods (Al-Khatib and Miller 1998, 2000; Miller and Al-Khatib 2002). IMI-R commercial hybrids were released to sunflower growers in 2003 (BASF 2003). However, there are concerns regarding gene flow of the IMI-resistance trait to wild species and possible ecological consequences. These concerns are justified because domesticated sunflower is an insect-pollinated species and is known to hybridize successfully with wild relatives. Furthermore, flowering of domesticated and wild sunflowers occurs sympatrically, pollinators are shared, and there are no strong reproductive barriers to prevent hybridization (Rieseberg et al. 1995a, 1995b; Schilling and Heiser 1981).

The cross-compatibility between domesticated sunflower

and wild relatives has been documented widely (Desrochers and Rieseberg 1998; Snow and Moran-Palma 1997; Snow et al. 1998; Whitton et al. 1997). In addition, Massinga et al. (2003) showed that resistance to imazamox was transferred from the IMI-R domesticated sunflower to common sunflower and prairie sunflower through pollen under field conditions. Up to 6% IMI-R plants were detected in wild plants at 30 m from domesticated IMI-R sunflower. Furthermore, artificial hybridization demonstrated that IMI resistance can be transferred from IMI-R sunflower species to their corresponding wild parents. That work suggests that feral sunflower species with acquired resistance to imazamox from IMI-R domesticated sunflower would be a source of successful secondary gene flow to susceptible plants, increasing the potential of further spread of IMI resistance. However, the persistence of IMI-resistant genes in subsequent generations will depend on the mode of inheritance and relative plant fitness, which includes plant vigor, biomass, seed production, seed dormancy, and competitiveness of the resistant plants (Arriola and Ellstrand 1997; Dale 1994).

Changes in fitness level are one of the potential effects of the escape of herbicide resistance from crops into wild plants. Fitness measures describe the potential evolutionary success of a genotype based on survival, competitive ability, and reproductive success, with the most fit individual leaving the greatest number of offspring and contributing a greater proportion of its genes to the gene pool of the population (Radosevich et al. 1997). Fitness differences between herbicide-resistant and herbicide-susceptible biotypes are usually inferred from comparisons of relative plant vigor, productivity, or competitiveness, as measured using specific traits including: seed dormancy, flowering date, seed production, aboveground biomass, and other factors that affect the likelihood of the survivorship and fecundity of the species (Radosevich et al. 1997; Warwick and Black 1994).

Gene flow from HRCs to wild species might confer a fitness advantage to wild plants resulting in more invasive and noxious weeds compared with their wild parents (Ellstrand et al. 1999; Snow and Moran-Palma 1997). Alternatively, introduction of herbicide-resistant genes also may result in growth and yield penalties (Mallory-Smith and Eberlein 1996). Although resistance to triazine herbicides conferred by the Ser to Gly change at Position 264 of the chloroplast D1 protein is known to reduce biomass, germination, or yield (Beversdorf et al. 1988; Conard and Radosevich 1979; Darmency and Pernès 1989), the situation with plant resistance to ALS-inhibiting herbicides is less clear. Marshall et al. (2001) reported no difference in photosynthesis, leaf area, height, or dry weight between imazethapyr-resistant and imazethapyr-susceptible common sunflower. Alcocer-Ruthling et al. (1992) found no differences in canopy height, plant biomass, or seed yield between sulfonylurea-susceptible (SU-S) and sulfonylurea-resistant (SU-R) kochia [*Kochia scoparia* (L.) Schrad.]. Thompson et al. (1994) observed that SU-R biotypes of kochia accumulated more biomass than their susceptible counterparts. Dyer et al. (1993) observed that SU-R kochia germinates more rapidly than the susceptible plants in the absence of herbicide. These findings suggest that ALS-resistant traits can provide plants with advantageous or neutral effects. It further indicates that the relative fitness of herbicide-resistant plants compared with their nonresistant counterparts cannot be generalized and factors such as genotype, population, geographical variability, intra- and interbiotype competition, environmental factors, and management practices should be taken into consideration (Warwick and Black 1994).

To fully understand the risks associated with the escape of the IMI-R trait, it is important to evaluate whether this trait confers any change in fitness to the wild species. The objectives of this study were to compare the growth of IMI-R common and prairie sunflowers and their corresponding imazamox-susceptible (IMI-S) plants under noncompetitive and competitive conditions and evaluate dormancy of IMI-R and IMI-S achenes.

Materials and Methods

Plant Material

Common sunflower and prairie sunflower were used in this study because these species occur in close proximity to domesticated sunflower throughout the central and western United States and they can acquire herbicide resistance by hybridizing with the domesticated IMI-resistant sunflower (Massinga et al. 2003). Both species are annual, self-incompatible, and diploid ($n = 17$) (Seiler and Rieseberg 1997).

Common sunflower achenes were collected from plants growing near the Konza Prairie Research Natural Area in northeast Kansas, where no herbicide had been applied in the past 25 yr. Achenes of prairie sunflower were obtained from the USDA-ARS North Central Regional Plant Introduction Station at Ames, IA. The IMI-resistant domesticated sunflower hybrid, CMS HA 425/RHA426 and CMS HA 89/RHA 409, an IMI-S genotype, closely related to CMS HA 425/RHA426 was provided by the USDA-ARS Sunflower Research Unit of the Crop Science Laboratory at Fargo, ND.

Achenes from common sunflower and prairie sunflower were germinated as described by Al-Khatib et al. (1998). Seedlings were then transplanted into 15-cm-diam pots filled with mixture of soil and sand (1:1, v/v). The soil was a Morrill loam (mesic typic Argiudoll) with pH 7.0 and 1.7% organic matter. Plants were fertilized weekly with a solution containing 300 $\mu g\ L^{-1}$ N, 250 $\mu g\ L^{-1}$ P, and 220 $\mu g\ L^{-1}$ K. Greenhouse conditions were 25/20 C day/night temperature and 16/8 h day/night photoperiod. Supplemental light was at 80 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux. IMI-R and IMI-S domesticated sunflowers were directly planted into 33-cm-diam pots.

Greenhouse Study

Ten plants of both feral species were selected, from these plants, five flower heads per plant were chosen randomly and hand-pollinated with pollen from the IMI-R domesticated sunflower hybrid to produce IMI-R common and prairie sunflower hybrids. An additional five flower heads on those same females were pollinated with pollen from the IMI-S domesticated sunflower hybrid to produce IMI-S common and prairie sunflower hybrids. Pollen was collected from heads of the domesticated sunflower into bags and applied gently with a brush to the surface of the stigmas of the wild species flowers without emasculation (Fick 1978). A subsample of 1,500 achenes for each hybrid, produced by crossing the IMI-R male with common and prairie sunflow-

er females, was germinated and grown in 15-cm-diam pots as described above. At the two- to three-leaf stage, plants were treated with 40 g ai ha^{-1} imazamox plus 0.25% (by volume) nonionic surfactant[1] to screen for resistance. Herbicide was applied with a bench-type[2] sprayer equipped with 80015LP tip[3] nozzles calibrated to deliver 187 L ha^{-1} at 138 kPa.

Visual injury was estimated 14 d after planting (DAP) on a scale of 0 to 100% where 0% indicates no injury and 100% indicates plant death. The plants of both common and prairie sunflower with less than 20% imazamox injury were classified as IMI-R and allowed to grow in the greenhouse in 15-cm pots. Plants resulting from crosses between the domesticated IMI-S male with common and prairie sunflower females were not screened for IMI resistance but were treated the same in all other respects. Because of the high degree of self-incompatibility among sunflower species and the high pollen load used in crossing, self-pollination events were negligible (Fick 1978). On all hybrids, photosynthesis, plant height, leaf area, leaf dry weight, stem dry weight, and total dry weight were determined 20, 30, 40, 50, and 60 DAP. Although imazamox is not known to have direct effects on photosynthesis and leaf area, these variables were studied to determine the effect of IMI-R genes on photosynthetic capacity that ultimately will affect plant fitness (Marshall et al. 2001).

Photosynthesis was measured on the third fully expanded leaf from the top using a LI-COR 6400 portable photosynthesis system.[4] Total leaf area was measured with a LI-COR 3100 area meter.[4] Plant parts were clipped, separated, and dried at 65 C for 48 h and weighed. Whole-plant aboveground biomass was then determined. Relative growth rate (RGR) and net assimilation rate (NAR) were calculated using the methods described by Hunt (1978).

Achene Germination Study

Achene germination was tested for IMI-R and IMI-S hybrids of common and prairie sunflower. Ten days after harvest, 10 achenes of each accession were planted in 15-cm-diam pots. Achene germination was determined 10, 30, 60, and 90 DAP. Achenes were considered germinated if the hypocotyl had emerged above the soil surface. Soil and growth conditions were as described above. At each rating date, germination was recorded and the soil from pots was emptied in a tray and screened. Achenes that did not germinate were removed and sterilized with 10% sodium hypochlorite solution for 20 min and rinsed thoroughly with distilled water before being scarified by removing approximately 2 mm of seed coat from the widest portion of each achene. To interrupt dormancy, scarified achenes were vacuum infiltrated with 0.3 μM gibberellic acid solution for 5 min, then placed on paper towels moistened with 0.3 μM gibberellic acid solution, and incubated in the dark at 25 ± 1 C for 24 to 48 h. Immediately after radical appearance, seed coats were removed, and seedlings were placed on new paper towels moistened with distilled water (Al-Khatib et al. 1998). The seedlings were incubated in a growth chamber for 48 h. The growth chamber conditions were 25/20 C day/night temperature, 16/8 h day/night photoperiod, and 550 ± 20 μmol m^{-2} s^{-1} photosynthetic photon flux.

Field Studies

Achenes of IMI-R and IMI-S hybrids were germinated and screened for IMI resistance as described above. Seedlings were transplanted in the greenhouse into 15-cm-diam pots filled with 500 g of soil. Soil and growth conditions were similar to those described above. In 2001, the experiment was conducted at Ashland Bottoms Research Farm located 12 km south of Manhattan, KS, and in 2002, experiments were conducted at the Kansas State University Agronomy Department Research Farm at Manhattan, KS, and Ashland Bottoms Research Farm. The soil types were a Haynie sandy loam (coarse-silty, mixed, calcareous, mesic, Mollic Udifluvent) with 6.1 and 5.9 pH and 3.2 and 2.4% organic matter at Ashland Bottoms in 2001 and 2002, respectively, and a Smolan silt loam (fine, montmorillonitic, mesic, Pachic Argiustoll) with pH of 6.5 and 2.7% organic matter in 2002 at Manhattan.

At the two- to three-leaf stage, hybrid seedlings of common and prairie sunflower were transplanted to the field on May 25, 2001, at Ashland Bottoms and May 15 and May 20, 2002, at Ashland Bottoms and Manhattan, respectively. Individual plots were 10-m long with four rows. Plants were spaced 25 cm within and 50 cm between rows. Plants were irrigated as needed, and plots were maintained weed free by hoeing. Plots were arranged in a conventional replacement series within a randomized complete block design (Radosevich 1987). Plants were established at the following IMI-R:IMI-S mixture ratios: 10:0, 7:3, 5:5, 3:7, and 0:10. Treatments were replicated four times for common sunflower and three times for prairie sunflower because of seed limitations.

Common and prairie sunflower growth and development were monitored throughout the 2001 and 2002 growing seasons. Plant height was measured 90 d after transplanting. Days to flower for each hybrid in a given mixture proportion were recorded as the number of days required for at least one plant of that hybrid to flower within the mixture proportion. Flower heads were harvested from the two central rows of each plot as they matured to prevent seedheads from shattering. At each harvest, number of heads and weight of 100 achenes were determined. Because both common and prairie sunflower have an indeterminate growth habit, they were allowed to remain in the field until the first frost, and then plants from the central two rows were cut at the soil surface. Plants were dried at 70 C for 72 h and weighed. Total seed weight was determined by adding the seed weight obtained in each harvest.

The competitive ability of IMI-R and IMI-S common and prairie hybrids was measured using the relative crowding coefficient (RCC) of total biomass and achene production of both hybrids (Novak et al. 1993). The RCC is a measure of the competitive ability of one genotype to obtain limiting resources when grown in mixtures with another genotype, compared with its ability to use those resources when grown in a pure stand. On the basis of this definition, an RCC > 1 indicates that the IMI-R hybrid is more competitive than the IMI-S hybrid. Conversely, an RCC < 1 indicates that the IMI-S hybrid is more competitive than the IMI-R hybrids, and an RCC of 1 indicates that IMI-R and IMI-S hybrids are equal competitors. The RCCs for total biomass and yield (Y) were calculated according to the following equation:

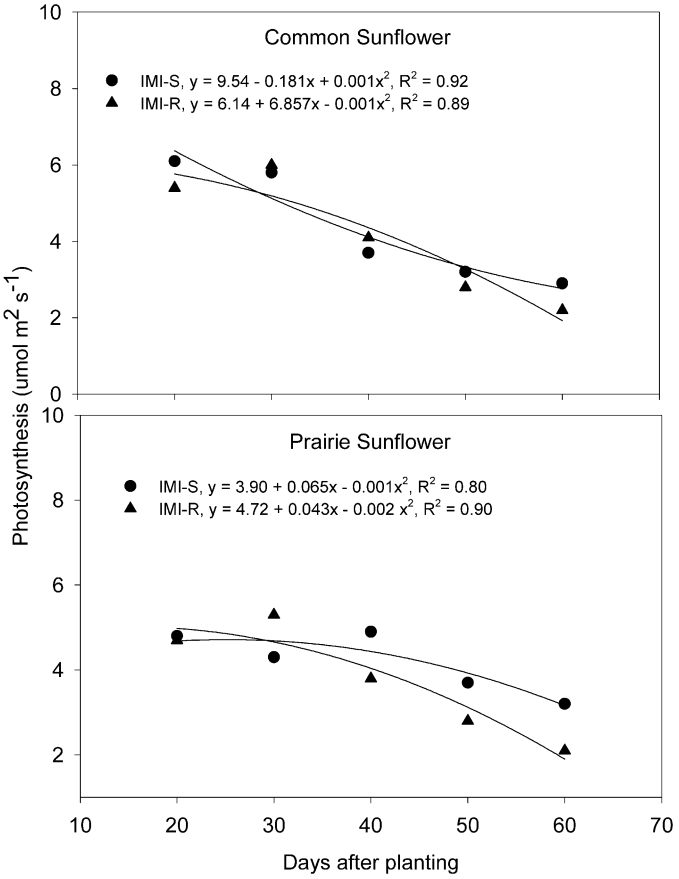

FIGURE 1. Photosynthesis of imazamox-resistant (IMI-R) and imazamox-susceptible (IMI-S) common and prairie sunflower hybrids grown under noncompetitive conditions.

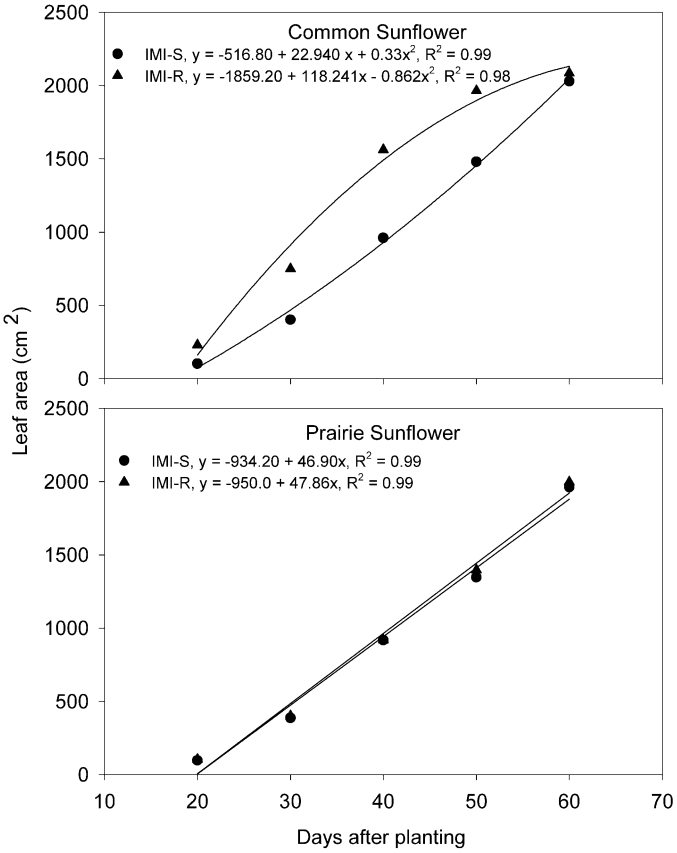

FIGURE 2. Plant leaf area of imazamox-resistant (IMI-R) and imazamox-susceptible (IMI-S) common and prairie sunflower hybrids grown under noncompetitive conditions.

$$\frac{Y_{(7:3\ \text{IMI}\ -\ \text{R})}}{Y_{(7:3\ \text{IMI}\ -\ \text{S})}} + \frac{Y_{(5:5\ \text{IMI}\ -\ \text{R})}}{Y_{(5:5\ \text{IMI}\ -\ \text{S})}} + \frac{Y_{(3:7\ \text{IMI}\ -\ \text{R})}}{Y_{(3:7\ \text{IMI}\ -\ \text{S})}} + \frac{Y_{(10:0\ \text{IMI}\ -\ \text{R})}}{Y_{(10:0\ \text{IMI}\ -\ \text{S})}} \quad [1]$$

Experimental Designs and Data Analysis

Experiments were conducted as randomized complete block designs. Greenhouse treatments were replicated four times. Field treatments were replicated four times for common sunflower, three times for prairie sunflower, conducted at one location in 2001 and at two locations in 2002. Treatments for the seed germination study were replicated eight times, and the study was repeated twice. Photosynthesis, plant height, and leaf area were analyzed using regression analysis. Regression slope and *y* intercepts were compared using *t* ratios (Draper and Smith 1998). Leaf dry weight, stem dry weight, total dry weight, achene germination were analyzed using analysis of variance, and mean differences between IMI-R and IMI-S hybrids were separated at $P \leq 0.05$ (Gomez and Gomez 1984).

Results and Discussion

Greenhouse Study

In general, photosynthesis rates of IMI-R and IMI-S common sunflower hybrids were similar at all sampling dates (Figure 1). However, the rate of photosynthesis in IMI-S prairie sunflower plants was slightly higher than in IMI-R plants, except at 30 DAP, when the photosynthesis rate was higher in IMI-R plants. The leaf area in IMI-R common sunflower was significantly greater than in IMI-S hybrids during the most rapid growth phase of the study (30 to 50 DAP); however, those differences disappeared by 60 DAP (Figure 2). In contrast, leaf area of IMI-R and IMI-S prairie sunflower hybrids was consistently similar. Plant height of IMI-S common sunflower was greater than IMI-R plants 50 and 60 DAP, whereas in prairie sunflower, height of IMI-S and IMI-R plants was similar (Figure 3). In both species, leaf weight and total dry weight of IMI-R and IMI-S hybrids were statistically identical (data not shown). Although IMI-S common sunflower plants were taller than the IMI-R plants, IMI-S plants did not produce greater biomass as might be expected because IMI-R plants had thicker branches and a larger number of branches compared with IMI-S plants. In both species, the lack of large differences in the rate of photosynthesis coupled with similar leaf areas at plant maturity and equivalent biomass production suggest that the photosynthetic capacity of IMI-R and IMI-S hybrids is similar.

RGR and NAR were similar in IMI-R and IMI-S common and prairie sunflower hybrids (Table 1). These results are in agreement with an earlier report by Marshall et al. (2001), which showed that the effects of IMI resistance on weed species are inconsistent. Marshall et al. (2001) reported no differences in growth parameters between IMI-R and

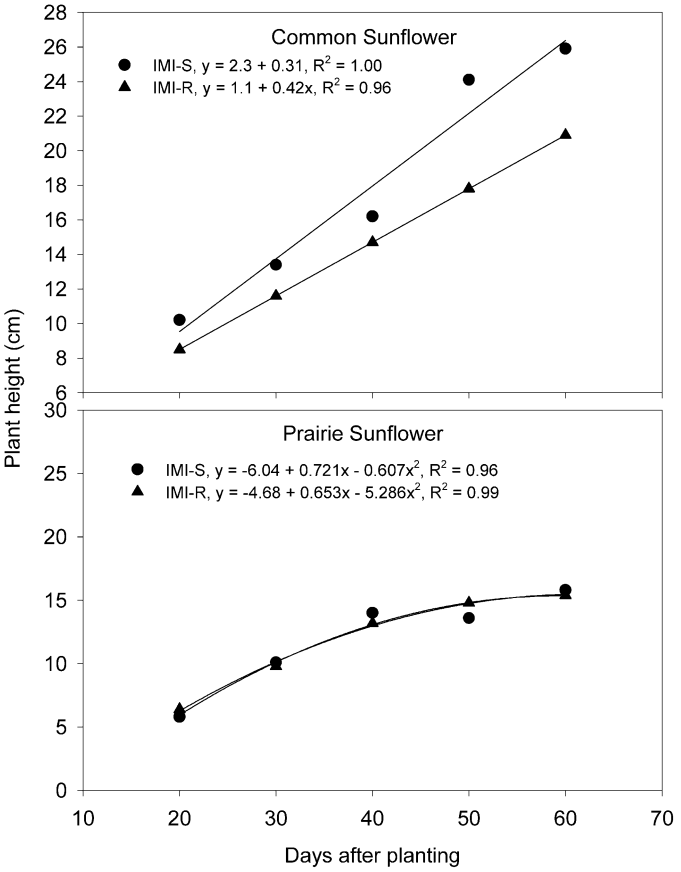

FIGURE 3. Plant height of imazamox-resistant (IMI-R) and imazamox-susceptible (IMI-S) common and prairie sunflower hybrids grown under noncompetitive conditions.

IMI-S common sunflower but observed high growth rate at early growth stages of resistant plants. In contrast, Poston et al. (2002) observed that one IMI-S and four IMI-R biotypes of smooth pigweed (*Amaranthus hybridus* L.) had similar NAR and RGR, but at early growth stages the IMI-S biotype had greater growth rate.

Achene Germination

In general, achene germination of IMI-R and IMI-S was similar in both common and prairie sunflower. No IMI-S hybrid common sunflower achenes germinated by 10 DAP. However, achene germination was 2, 8, and 2% at 30, 60, and 90 DAP, respectively (data not shown). In contrast, no IMI-S hybrid prairie sunflower achene germinated throughout the experiment. In IMI-R common sunflower, 3, 12, 2, and 8% of achenes germinated 10, 30, 60, and 90 DAP, respectively. In IMI-R prairie sunflower, 3, 0, 1, and 0% germination was observed 10, 30, 60, and 90 DAP, respectively. However, percent germination of all achenes at each time period was increased when achenes were scarified and treated with 0.3 μM gibberellic acid. Induced germination reached 43 and 67% in IMI-S and IMI-R achenes of common sunflower and 47% and 41% in IMI-S and IMI-R achenes of prairie sunflower, respectively.

Snow et al. (1998) observed that hybrids of crop and wild common sunflower had 90 to 95% achene germination, whereas achene germination of wild plants from two different regions ranged from 64 to 74%. Furthermore, they observed that crop–wild hybrid achenes germinated earlier than seeds from wild plants. Much lower germination rates were observed in this study for hybrids of domesticated by common sunflower and especially for hybrids of domesticated by prairie sunflower. An ideal approach to determine whether differences between herbicide-resistant weeds and their feral counterparts are due to the herbicide-resistance trait or the genetic background is to use near-isogenic lines. The use of near-isogenic lines minimizes the number of genes that differ between tested lines. In this study, female and male plants of domesticated sunflower, with and without the IMI-resistance trait, were used to create crop by wild hybrids. The IMI-R female parent had HA 89 as the recurrent parent in crosses with the wild, resistant source to create CMS HA 425. CMS HA 89 was the female of the IMI-S. The IMI-R male parent had RHA 409 in crosses to create the line RHA 426. RHA 409 was the male of the IMI-S hybrid. Both hybrids, therefore, have a majority of their genes in common. However, genetic differences do exist between the two male lines and may have contributed to some of the differences between IMI-R and IMI-S hybrids in this study. Similarly, Thompson et al. (1994) and Alcocer-Ruthling et al. (1992) observed that SU-R kochia and prickly lettuce (*Lactuca serriola* L.) germinated faster than SU-S biotypes. However, the differences between the SU-R and SU-S biotypes were suggested to be because of genetic polymorphism and not because of the resistance trait.

Sunflowers have annual dormancy cycles dependent on fluctuations in environmental conditions (Connor and Hall 1997). The results of this study show that achenes from IMI-R and IMI-S plants displayed a high degree of dormancy. This could provide an advantage for IMI-R hybrids because dormant achenes can remain in the soil and germinate later, maintaining a source of IMI resistance in the environment over a longer period of time. In contrast, nondormant seedlings that emerge early will be eliminated during seedbed preparation by cultivation or herbicide application.

TABLE 1. NAR and RGR of IMI-R and IMI-S common and prairie sunflower hybrids grown in the greenhouse.[a]

	NAR				RGR			
	Common sunflower		Prairie sunflower		Common sunflower		Prairie sunflower	
Interval	IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S
DAP	mg cm^{-2} day^{-1}				mg g^{-1} day^{-1}			
20 to 30	1.5	5.7*	4.7	5.1	3.1	3.2	3.7	3.6
30 to 40	4.1	4.6	3.7	2.7	4.0	3.8	3.8	3.9
40 to 50	0.8	2.7	0.8	0.8	4.1	3.9	3.9	3.9
50 to 60	4.7	4.7	0.9	1.0	4.8	4.7	4.1	4.1

[a] Abbreviations: DAP, days after planting; IMI-R, imazamox resistant; IMI-S, imazamox susceptible; NAR, net assimilation rate; RGR, relative growth rate.

* Indicates that at a given interval the parameter differed significantly from the other hybrid ($P \leq 0.05$).

Field Study

Because treatment by year interactions were significant, data are presented by years. However, there were no signif-

TABLE 2. Mean (±SE) days to flower, plant height, heads per plant, and 100 achene weight of IMI-R and IMI-S common and prairie sunflower hybrids grown at different population mixture ratios in 2001 and 2002.[a]

IMI-R:IMI-S population ratio	2001							
	Days to flower		Plant height		Heads plant^{-1}		Weight 100 achene	
	IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S
	days		cm		no.		g	
	Common sunflower							
10:0	88 ± 7	—	187 ± 32	—	87 ± 11	—	0.81 ± 0.03	—
7:3	98 ± 7	87 ± 6	187 ± 28	162 ± 32	66 ± 11	59 ± 8	0.92 ± 0.03	0.73 ± 0.08
5:5	95 ± 7	90 ± 6	193 ± 28	160 ± 32	69 ± 11	65 ± 8	0.67 ± 0.03	0.68 ± 0.08
3:7	93 ± 7	98 ± 6	191 ± 28	178 ± 32	57 ± 11	71 ± 8	0.73 ± 0.03	0.57 ± 0.08
0.10	—	96 ± 6	—	161 ± 28	—	65 ± 8	—	0.70 ± 0.08
	Prairie sunflower							
10:0	76 ± 5	—	100 ± 21	—	105 ± 17	—	0.88 ± 0.09	—
7:3	65 ± 5	84 ± 19	103 ± 21	118 ± 25	101 ± 17	101 ± 10	1.00 ± 0.09	0.83 ± 0.07
5:5	70 ± 5	71 ± 19	96 ± 21	105 ± 25	99 ± 17	98 ± 10	0.87 ± 0.09	0.68 ± 0.07
3:7	72 ± 5	68 ± 19	104 ± 21	117 ± 25	103 ± 17	98 ± 10	0.67 ± 0.09	0.73 ± 0.07
0:10	—	71 ± 19	—	122 ± 25	—	95 ± 10	—	0.67 ± 0.07

2002							
Days to flower		Plant height		Heads plant^{-1}		Weight 100 achene	
IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S	IMI-R	IMI-S
days		cm		no.		g	
Common sunflower							
78 ± 5	—	166 ± 31	—	90 ± 17	—	0.51 ± 0.07	—
78 ± 5	82 ± 8	190 ± 31	152 ± 29	64 ± 17	51 ± 11	0.92 ± 0.07	0.68 ± 0.04
90 ± 5	90 ± 8	193 ± 31	140 ± 29	53 ± 17	55 ± 11	0.67 ± 0.07	0.48 ± 0.04
90 ± 5	95 ± 8	189 ± 31	198 ± 29	53 ± 17	61 ± 11	0.60 ± 0.07	0.65 ± 0.04
—	100 ± 8	—	177 ± 29	—	77 ± 11	—	0.79 ± 0.04
Prairie sunflower							
66 ± 9	—	107 ± 30	—	103 ± 14	—	0.39 ± 0.06	—
68 ± 9	94 ± 23	103 ± 30	123 ± 22	109 ± 14	107 ± 17	0.41 ± 0.06	0.25 ± 0.03
70 ± 9	74 ± 23	116 ± 30	112 ± 22	97 ± 14	97 ± 17	0.32 ± 0.06	0.32 ± 0.03
70 ± 9	77 ± 23	106 ± 30	131 ± 22	88 ± 14	108 ± 17	0.63 ± 0.06	0.25 ± 0.03
—	81 ± 23	—	121 ± 22	—	99 ± 17	—	0.39 ± 0.03

[a] Abbreviations: IMI-R, imazamox resistant; IMI-S, imazamox susceptible; SE, standard error.

icant interactions between treatment and locations; therefore, data were averaged across locations.

There was a significant hybrid by mixture ratio interaction indicating that the IMI-R and IMI-S plants responded differently to the various ratios or interhybrid competition. In 2001, IMI-R common sunflower plants were consistently taller than IMI-S plants. Height of IMI-R hybrids was greater than IMI-S hybrids as the number of IMI-R plants increased in the mixture (Table 2). However, days to flower, heads per plant, and 100 achene weight varied within the mixture ratios but did not show a consistent increase or decrease with change in the mixture proportion. In prairie sunflower, days to flower, heads per plant, and plant height of IMI-R and IMI-S plants were similar.

In 2002, IMI-S common sunflower growing alone, flowered 22 d later, was 11 cm taller, produced 13 fewer heads plant^{-1}, and produced larger achenes than a pure stand of IMI-R plants (Table 2). In mixed stands, regardless of the mixture proportion, IMI-S plants flowered consistently later than IMI-R plants, but the number of days to flower decreased with a greater number of IMI-R plants in the mixture. In addition, as the number of IMI-R plants increased, the number of heads per plant of IMI-S plants decreased, but plant height and weight of 100 achenes were similar. Days to flower in IMI-R plants increased from 78 in a pure stand to 90 at the 5:5 and 3:7 mixture proportions. Also, the number of heads per plant decreased as the competition from susceptible plants increased.

In prairie sunflower, IMI-S plants growing alone, flowered 15 d later, were 28 cm taller, produced 14 fewer heads plant^{-1}, and had smaller achenes than IMI-R plants growing alone (Table 2). These variables did not show a definitive trend with change in the mixture proportion, but heads per plant increased as the number of IMI-R plants increased in the mixture. Days to flower and height of IMI-R plants were not affected by changes in population mixture. However, heads per plant was greater at higher IMI-R:IMI-S ratios. In addition, weight of 100 achenes decreased as the number of IMI-R plants decreased in the population mixture.

Both IMI-R and IMI-S common and prairie sunflower hybrids produced the highest achene yields when grown in pure stands. As the proportion of IMI-S plants increased in the mixture, the achene production declined (Figure 4). Generally, the decline in achene production was greatest at population mixtures of 7:3. The IMI-S plants showed a more gradual decrease in achene production as the propor-

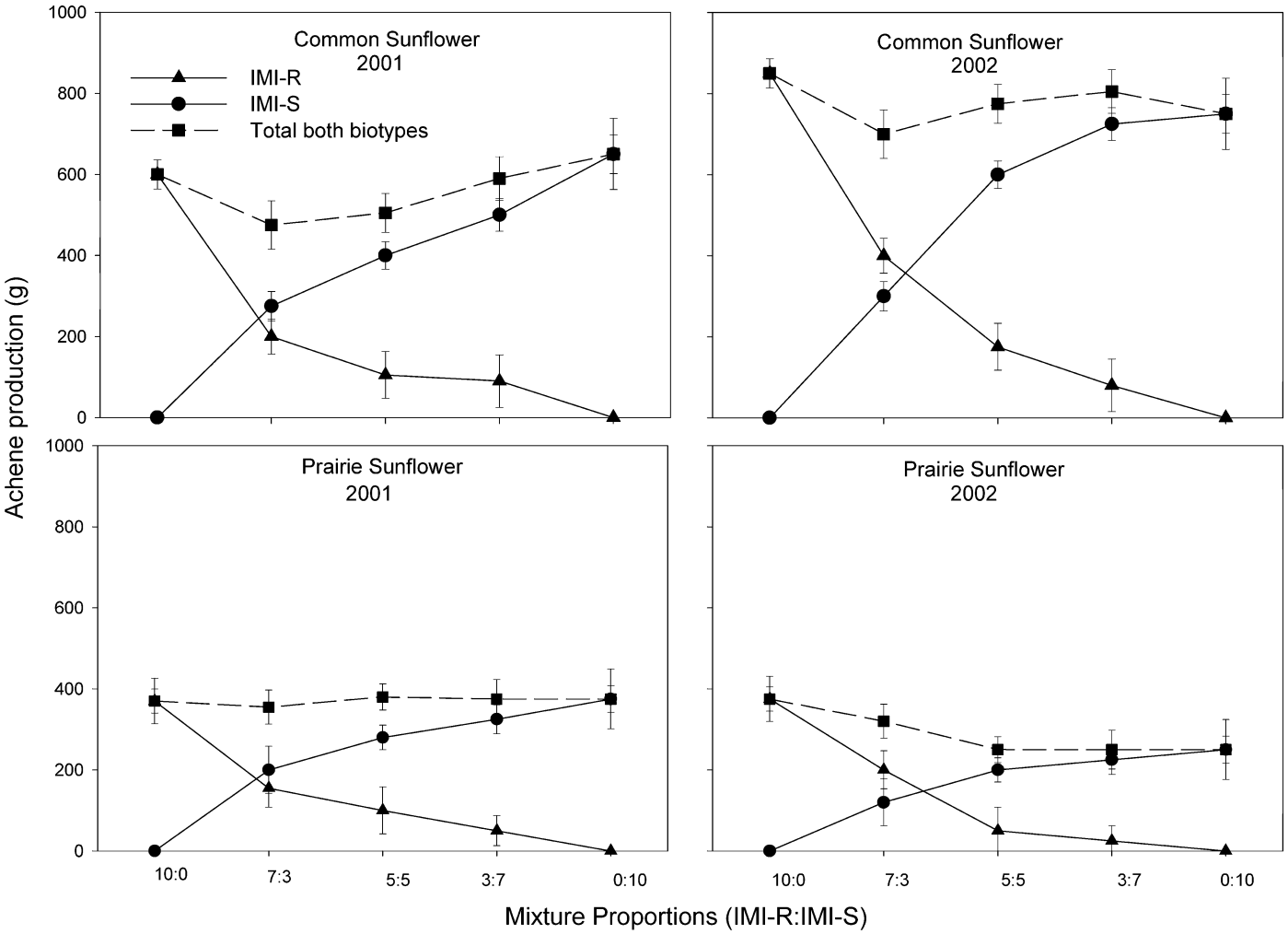

FIGURE 4. Replacement series diagrams for total achene yields of imazamox-resistant (IMI-R) and imazamox-susceptible (IMI-S) common and prairie sunflower hybrids of different IMI-R:IMI-S population mixtures. Bars indicate standard error.

tion of IMI-R plants increased in the mixture. This indicates that achene production of IMI-R plants was highly affected by the introduction of IMI-S plants. IMI-R plants were more robust and had a greater number of branches, suggesting that they would be more affected by intracompetition than by competition from IMI-S plants. Replacement series diagrams, such as Figure 4, illustrate competitive effects between tested plants. Equal competition between hybrids would be represented by straight lines across the mixture proportions, with the intersection at 50% of the mixture ratio, whereas curved lines shifting the intersection point away from the 5:5 mixture ratio indicate that competitive differences exist (Anderson et al. 1996).

In 2001, the intersection point for achene production in both common and prairie sunflower was shifted toward the 7:3 (IMI-R:IMI-S) ratio, indicating that IMI-S hybrids were more competitive (Figure 4). In 2002, the intersection point for common and prairie sunflower is shifted closer to the 5:5 IMI-R:IMI-S ratio, indicating more equal competition between IMI-R and IMI-S common sunflower hybrids. The differences between 2001 and 2002 suggest that the outcome of the competition between IMI-R and IMI-S hybrids of common and prairie sunflower depends more on environmental conditions than on genetic differences.

The RCC values for achene production ranged between 0.9 and 1.3 but were not significantly different from 1, indicating equal competitiveness between the IMI-R and IMI-S hybrids in both common and prairie sunflower. Similar results were observed for total plant biomass (data not shown).

This study showed that resistance to imazamox, in a domesticated by feral species hybrid background, did not reduce or improve the relative fitness of common or prairie sunflower hybrids compared with their IMI-S hybrids. Although, IMI-R plants began flowering earlier than IMI-S plants, both common and prairie sunflower species flower over a long period of time, allowing the flowering period of IMI-R and IMI-S plants to overlap.

Although no lasting or significant differences in relative fitness were observed between IMI-S and IMI-R hybrids, this study provides an estimate of the relative fitness of IMI-resistant common and prairie sunflower with useful implications for long-term management of IMI resistance in wild sunflowers. For example, the lack of differences between the

IMI-R and IMI-S sunflower fitness suggests that the frequency of IMI-R plants will likely remain constant if IMI herbicide application is discontinued or if IMI-R–domesticated sunflower cultivars are not used (Dale 1994; Radosevich et al. 1997). Furthermore, differences between years and species suggest that the frequency of IMI resistance in wild plants will depend on environmental conditions, local species mixtures, and the rate and amount of gene flow from cultivated fields into wild populations.

Sources of Materials

[1] X-77, a mixture of alkylaryloxyethylene, free fatty acids, glycols, and isopropanol, Loveland industries Inc., P.O. Box 1289, Greeley, CO 80632.

[2] Research Track Sprayer, DeVries Manufacturing, RR1 Box 184, Hollandale, MN 56045.

[3] 80015LP TeeJet Tip, Spraying Systems Co., P.O. Box 7900, Wheaton, IL 60189.

[4] LI-COR Inc., 4421 Superior Street, Lincoln, NE 68502.

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